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ARCTIC FOX INFLUENCE ON A SEABIRD COMMUNITY IN LABRADOR: A NATURAL EXPERIMENT

T. R. BIRKHEAD[1] AND D. N. NETTLESHIP[2]

ABSTRACT.—The Gannet Islands contain the single most important seabird colony in Labrador, both in terms of numbers and species diversity. In 1992, we discovered arctic foxes (*Alopex lagopus*) on these islands during the breeding season. Of five islands examined, two had resident foxes (in one case breeding), two had been visited by foxes earlier in the season, and one had no foxes and had not been visited. A comparison of these islands in 1992 and with our detailed studies from the early 1980s, revealed the effect that foxes had had on seabirds. On islands with foxes, Razorbills (*Alca torda*), Common Murres (*Uria aalge*), and Thick-billed Murres (*U. lomvia*) had ceased breeding. Atlantic Puffins (*Fratercula arctica*) continued to attempt to breed, but fox predation on adult birds and eggs was intense and breeding success low. On islands visited by foxes earlier in the season, the number of breeding Razorbills was reduced, and breeding by Common Murres was delayed by 2–3 weeks.

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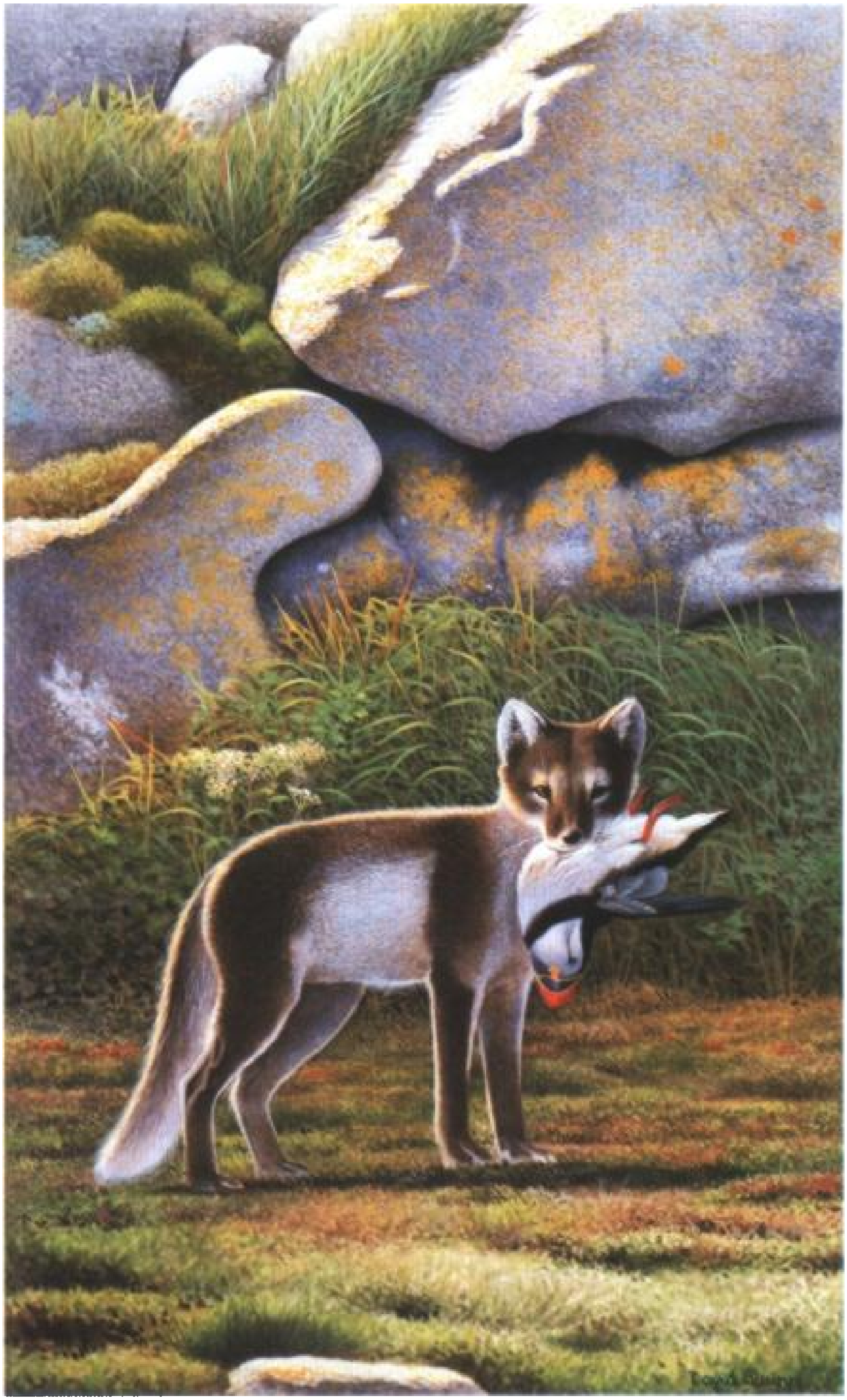
The selection of breeding areas by birds is determined mainly by the proximity of feeding areas and safety from predators (Lack 1968). There is good circumstantial evidence that marine birds breed on offshore islands and on steep mainland cliffs to avoid terrestrial predators (Larson 1960, Lack 1968). Where predators have been introduced to islands by man, ground-nesting seabirds have usually been rapidly extirpated (Moors and Atkinson 1984, Burger and Gochfeld 1994). For example, between 1750 and the 1930s arctic foxes (*Alopex lagopus*) and red foxes (*Vulpes vulpes*) were introduced to about 450 Alaskan islands for fox farming: their effect on the ground-nesting birds was disastrous (Sekora et al. 1979, Bailey 1993, Bailey and Kaiser 1993). In other areas where foxes and

[1] Dept. Animal & Plant Sciences, Sheffield Univ., P.O. Box 601, Sheffield S10 2UQ, England, U.K.
[2] Canadian Wildlife Service, Bedford Institute of Oceanography, P.O. Box 1006, Dartmouth, Nova Scotia, Canada B2Y 4A2. (Please send reprint requests to D. N. Nettleship.)



Arctic fox *Alopex lagopus* with Atlantic Puffin *Fratercula arctica* at the Gannet Islands, Labrador, 1992. Painting by David Quinn. [Editor's note: this painting has recently been stolen, and T. R. Birkhead would appreciate any information concerning its whereabouts.]

seabirds coexist, it is clear that the foxes have been a major factor influencing the habitat selection of the birds (Fisher and Lockley 1954, Larson 1960, Petersen 1982, Bailey 1993).

Although the end result of introducing foxes onto seabird islands is well known, the actual process by which it occurs has not previously been described. In the present paper, we describe the consequences of a natural invasion of arctic foxes onto a seabird colony in Labrador. Our study was unique in that the seabird colony at the Gannet Islands, Labrador, comprises several adjacent islands (Fig. 1), some of which held foxes and some which did not during our study. We thus had a 'natural experiment' in which we could determine which effects were the results of foxes and which were due to other causes.

STUDY AREA AND METHODS

The Gannet Islands (53°56′N, 56°32′W) constitute the largest and most diverse seabird colony in Labrador (Nettleship 1980, Nettleship and Glenn 1992). In 1983, when the most detailed census was conducted, the breeding seabird community at the Gannet Islands comprised the following: 13 pairs of Northern Fulmars (*Fulmarus glacialis*), about 14 pairs of Leach's Storm-Petrel (*Oceanodroma leucorhoa*), 100 pairs of Great Black-backed Gulls (*Larus marinus*), 52 pairs of Black-legged Kittiwakes (*Rissa tridactyla*), 4930 pairs of Razorbills (*Alca torda*), 38,350 pairs of Common Murres (*Uria aalge*), 965 pairs of Thick-billed Murres (*U. lomvia*), 35 pairs of Black Guillemots (*Cepphus grylle*), and 41,300 pairs of Atlantic Puffins (*Fratercula arctica*) (Nettleship et al. 1984, Birkhead and Nettleship 1987a). Northern Fulmars, Great Black-backed Gulls, and most Common Murres and Razorbills bred in open habitat relatively accessible to terrestrial predators. Leach's Storm-Petrels and Atlantic Puffins nested in earth burrows, and Black Guillemots nested in rock crevices under boulders. Only Black-legged Kittiwakes and Thick-billed Murres bred on cliff ledges. Prior to the present study, we had conducted detailed investigations of the reproductive ecology of the seabirds, particularly the alcids, at this colony between 1981 and 1983 (Birkhead and Nettleship 1983, 1987a,b,c, 1988; Birkhead et al. 1985a,b; D. N. Nettleship, unpubl. data).

The Gannet Islands comprise a total of seven small islands: a group of five adjacent islands (referred to as the Gannet Clusters and identified as GC1 through GC5 which lie within 500 m of each other, see Fig. 1), Western Gannet (also referred to as GC6) which lies 1.5 km to the west of GC1, and Outer Gannet which lies 7 km north of the Gannet Clusters (Fig. 1). The islands vary in area from 4.4 ha (GC4) to 125 ha (GC6). All are low-lying (maximum height: 66 m above sea level) and are mainly rocky with heath scrub vegetation. The nearest point on the mainland is at Grady, about 17 km away.

In general, the summer (July–August) climate along the Labrador coast is cool: mean daily temperatures are about 10°C. Between December and late May, the sea ice is extensive and continuous from beyond the Gannet Islands to the adjacent mainland and to the north (Birkhead and Nettleship 1987a). The observations recorded here were made in July and August 1992 during which time temperatures on the Labrador coast were particularly low (Atmospheric Environmental Service, Environment Canada, Cartwright), possibly associated with the eruption of Mount Pinatuba in the Phillipines which is thought to have caused a global decline in temperatures through an increase in aerosols (Kerr 1993).

The present study was made on the Gannet Clusters (GC1 through to GC5) between 30

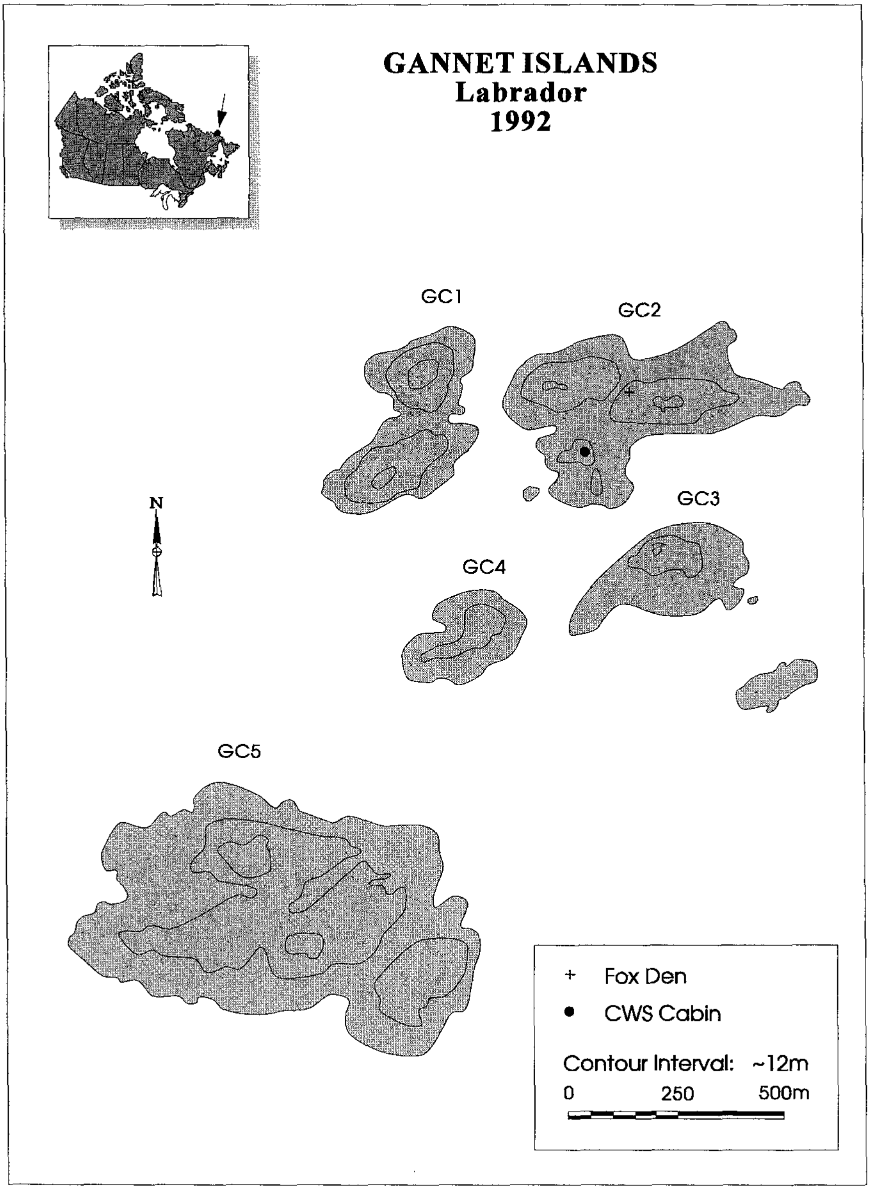


FIG. 1. Sketch map of five of the seven islands comprising the Gannet Islands (GC1 to GC5), Labrador, showing the approximate locations of the arctic fox den found on GC2 in 1992 and the main CWS research cabin. Inset map shows general location of the Gannet Islands archipelago in eastern Canada.

July and 13 August 1992. Previously, during the early to mid 1980s, we had documented the timing of breeding and breeding success of seabirds at the Gannet Clusters using standardized techniques (Nettleship 1976; Birkhead and Nettleship 1980; Birkhead and Nettleship 1987a,b,c). During the present study, we collected information that allowed us to make comparisons with information obtained in the 1980s and to determine the effect of arctic foxes on breeding performance of the seabirds. We also compared the breeding biology of seabirds in 1992 on those islands with and without foxes.

RESULTS

In 1992, there were resident foxes on GC2: a breeding pair and their two 8–10 week-old offspring. On GC5 there were two adult foxes, but we found no evidence of breeding. At the time of our visit, there were no foxes on GC1, GC3 or GC4, but we obtained clear evidence that foxes had been on GC4, circumstantial evidence that foxes had been on GC3, and no evidence whatsoever that foxes had been on GC1.

Prior to our observations in 1992, there were no records of arctic foxes spending the summer months on any of the Gannet Islands, even though the islands have been examined from the 1920–1930s (Austin 1932, Todd 1963) and 1950s (Tuck 1953, 1961), through the 1970s (1972, 1978, 1979) to the mid 1980s (Nettleship 1980, 1981; Birkhead and Nettleship 1983; Nettleship and Evans 1985; Birkhead and Nettleship 1987a,b,c). According to local people, arctic foxes occur regularly on the adjacent mainland during the winter months (Brice-Bennett 1977; see also Banfield 1974, Nowak 1991), but all observers (including Cartwright 1792, Townsend 1911, Harper 1960, Brice-Bennett 1977) also point out that arctic foxes usually disappear (in a northerly direction) again in the spring. It seems likely that arctic foxes move south in Labrador during the winter, sometimes traveling over the sea ice, and in this way reached the Gannet Clusters. We do not know when the foxes we observed in 1992 first reached the Gannet Islands, but circumstantial evidence suggests that it might have been several winters prior to the 1991–1992 season. There was an influx of arctic foxes onto the north shore of the Gulf of St. Lawrence during the winter of 1987–1988 (G. Chapdelaine, pers. comm., CWS-Quebec Region files), associated with particularly heavy ice. It is possible that the foxes we observed also arrived on the Gannet Islands during that winter (see below).

Our camp was on GC2 where we were able to observe the foxes directly. They spent much of their time in the Atlantic Puffin subcolony searching for eggs and adults. Although we saw them obtain eggs on numerous occasions, we did not witness foxes capturing or killing adult puffins (Frontispiece). We did, however, see foxes carrying recently killed puffins and found numerous freshly dead adult puffins and a fox cache comprising 26 Atlantic Puffins, three Common Murres, and two Razorbills. We also found two dead Razorbills, which we presumed to have been killed by foxes, under boulders in their breeding colonies.

Seabird Breeding Biology

There was no evidence of any recent or past presence of arctic foxes on GC1 in 1992, so we have used the biology of the seabirds on this island as our baseline against which to compare the other islands.

Common Murre.—We had no previously established study plots on GC1 so we were unable to make any quantitative comparisons of the proportion of sites occupied in 1992 compared with the 1980s. However, our subjective impression, and comparisons of photographs taken in the 1980s, indicated that there had been no reduction in the number of breeding Common Murres. On 3 August, we examined one group of breeding Common Murres considered typical of the GC1 murre population and found 106 chicks and 48 eggs; thus by this date 69% of eggs had hatched. We measured the wing length of 57 chicks and found the mean to be 33.82 mm ± 4.85 SD, and the longest wing length 44 mm. Comparison of standard growth curves obtained in the 1980s for Common Murre chicks at the Gannet Islands (T. R. Birkhead and D. N. Nettleship, unpubl. data) indicated that the chick with the longest wing length was 10 days old and had therefore hatched on 28 July. In the 1980s, the mean interval between first hatching and the median hatching date was 6 days (range: 4–9 d). Assuming that the first hatching date in 1992 was 28 July, the median hatching date was around 3 August 1992.

Thick-billed Murre.—Counts of Thick-billed Murres in 1992 showed that their numbers on GC1 (and elsewhere on the Gannet Clusters) had increased substantially since the 1980s (D. N. Nettleship and T. R. Birkhead, unpubl. data). Casual inspection of chicks on breeding ledges during feeding observations (without disturbing birds from ledges) revealed 19 eggs and 19 chicks on 8 August, which suggests that the median hatching date was around this time.

Razorbill.—In the 1980s, we established two Razorbill study plots on the northern end of GC1. On 3 August 1992, we examined one of these to determine the proportion of sites occupied by breeding birds and the proportion of eggs and chicks. (The other study plot was not examined in detail to avoid disturbing the large numbers of Common Murres breeding close by.) We found that all 110 Razorbill breeding sites identified in the 1980s were occupied and that there were an additional 11 occupied sites within the boundaries of the study plot. There were 93 eggs and 28 chicks: 23% chicks, most of which we estimated to be about 1–3 days old. We therefore assumed that the first chicks had hatched on 31 July. In the 1980s, the mean interval between first and median hatching dates

TABLE 1
TIMING OF BREEDING OF ALCIDS AT THE GANNET ISLANDS, LABRADOR, IN THE EARLY 1980S AND IN 1992[a]

Species	Median hatching 1981–1983	Median hatching 1992
Razorbill	23 July–4 August	9 August
Common Murre	16–26 July	3 August
Thick-billed Murre	22–28 July	3 August
Atlantic Puffin	30 July–10 August	14 August

[a] Values given are the range of median hatching dates for the 1980s and the estimated median hatching dates for birds undisturbed by arctic foxes on Island GC1 in 1992 (see text).

was nine days (D. N. Nettleship and T. R. Birkhead, unpubl. data), so we assumed that in 1992 the median hatching date for Razorbills on GC1 was 9 August.

Atlantic Puffin.—In the 1980s, the density and occupancy of Atlantic Puffin burrows were determined in 10 areas on GC1. In 1992, on 11 August, five of those areas were re-examined. We found 151 of 176 (89%) burrows to contain either an egg (N = 143) or a newly hatched chick (N = 8). All eight chicks were probably less than one day old (based on wing length), and four were still wet, indicating that they had only recently hatched. We therefore assumed that the first chicks hatched on 11 August in 1992. In our previous studies, we found that the mean interval between first and median hatching dates was three days (D. N. Nettleship and T. R. Birkhead, unpubl. data), so we estimated that the median hatching date in 1992 was 14 August.

Table 1 shows the estimated timing of breeding of four alcid species on GC1 in 1992 and compares these values with those obtained in the 1980s. It is clear from these comparisons that the timing of breeding in 1992 was considerably later than we had previously recorded. Razorbills and Common Murres were between one and two weeks later than in the 1980s, and Thick-billed Murres and Atlantic Puffins about one week later. Presumably the delay in breeding was associated with the relatively low summer temperatures in 1992.

The Effects of Arctic Foxes on Seabirds on Islands GC2 and GC5

Island GC2.—In 1992, a pair of arctic foxes and their two offspring were present on GC2. In the 1980s, we recorded 1219 pairs of breeding Razorbills in five subcolonies on this island, but in 1992 all Razorbill subcolonies were abandoned. The adult birds spent most of their time in rafts on the sea directly opposite their subcolony location. Occasionally in the evening, Razorbills alighted on rocks adjacent to the subcolonies, but they were nervous and rarely stayed long. We found one whole Razorbill egg (apparently deserted) and the remains of 12 other egg shells at breeding sites in the subcolonies, indicating that some birds had attempted to reproduce in 1992. We also found Razorbill eggs (none of which showed signs of incubation) and dead adult Razorbills which had been cached by foxes. Judging from the vegetation in the Razorbill colonies, especially around the individual breeding sites, it was clear that many sites had not been used in either the 1992 season or in one or more seasons before that, which suggests that foxes might have been present on GC2 for several seasons.

Also on GC2 in 1983, we recorded 50 pairs of Common and 19 pairs of Thick-billed Murres, but in 1992 we found no murres breeding on GC2. There was no evidence that Common Murres were visiting their breeding colonies in 1992. However, the Thick-billed Murre breeding ledges had large amounts of conspicuous pink guano, typical of this species elsewhere on the Gannet Clusters, indicating that they had been regularly visited. Indeed, on a number of occasions adult Thick-billed Murres were seen on these ledges. The Common Murre breeding sites on GC2 were similar to those of the Razorbill, located in low-lying boulder areas and hence extremely accessible to foxes. The Thick-billed Murre breeding areas on GC2 were located on a steep cliff, but a deep crack running from the top of the island past the breeding ledge made the ledge readily accessible to humans and hence presumably foxes.

In the 1983 census of GC2, we had also recorded 13 breeding pairs of Northern Fulmars but found none in 1992. Indeed, we saw only a single adult fulmar, far offshore from the Gannet Islands, during our entire visit in 1992. In 1983, we recorded 12 pairs of Black Guillemots breeding on GC2, whereas none appeared to be breeding in 1992 although birds were seen regularly on the water (maximum count: 24 individuals).

In 1983, the breeding population of Atlantic Puffins on GC2 was estimated to be 6192 pairs (Nettleship et al. 1984). In 1992 on 9 August, a sample of 112 burrows was examined. Of these, 41 (36.6%) were empty and inactive and 71 (63.4% burrow occupancy) contained either nest material or an egg or shell fragments and were assumed to have been occupied during the 1992 season. Of the 71 active burrows, only 13 (18.3%) contained an egg. Comparable values for 1983 were 77.6% burrow occupancy (280 of 356 burrows), with 40% of these active burrows with an egg or chick. Differences between years for burrow occupancy and nest status were highly significant ($P < 0.001$), with rates lower in 1992 when foxes were present than in 1983 when they were not (occupancy: $\chi^2 = 10.58$, 1 df; nest status: $\chi^2 = 11.62$, 1 df).

Island GC5.—On GC5 where there were two resident adult arctic foxes the effect on the seabirds was similar to that on GC2. Where we had found 1213 pairs of Razorbills in 1983, we found just two breeding pairs in 1992. Both of these were incubating on small ledges on a steep cliff and were presumably inaccessible to the foxes. We also found one partly eaten adult Razorbill and remains of five Razorbill eggs, along with several hundred predated puffin and murre egg shells. Where there had been approximately 250 breeding pairs of Common Murres in 1983, there was none breeding in 1992. The estimated number of Atlantic Puffins breeding on GC5 in 1983 was 7,780 pairs. In 1992 a sample of 117 burrows was examined on five plots on 11–12 August, of which 60 (51.3%) were empty and had apparently not been used in the 1992 season and a further 57 (48.7%) were active and contained either nest material or an egg. Of the 57 active burrows 14 (24.6%) contained an egg; no eggs had hatched. Comparable figures for 1983 were 92.9% burrow occupancy (N = 365) with 234 of 339 active burrows (69%) with eggs or chicks. These inter-year differences for puffins were highly significant ($P < 0.001$) with burrow occupancy and sites with an egg or chick (nest status) much higher in 1983 than 1992 when foxes were present (occupancy: $\chi^2 = 117.86$, 1 df; nest status: $\chi^2 = 41.22$, 1 df).

The Effects of Arctic Foxes on Seabirds on Islands GC4 and GC3

Island GC4.—There were no foxes present on this island during our visit, but the presence of fox scats, cached Common Murre eggs (N = 6) and Atlantic Puffin eggs (N = 4), a cached adult puffin, and the corpses of adult puffins made it clear that foxes had been present earlier in the season.

In 1983, we established three Razorbill study plots (A, B, C) on GC4, and these were re-examined in 1992. Plot A, which had 45 active sites in 1983, contained just seven eggs and 13 empty sites on 4 August 1992. Plot B (43 sites in 1983) contained six eggs and 17 empty sites on 4 August 1992, and Plot C (25 sites in 1983) contained nine eggs and 16 empty sites between 4 and 13 August. Overall, we estimated that about 20% of the sites occupied by Razorbills in 1983 were being used in 1992. As with GC2 and GC5, our impression was that numbers of adult birds near the GC4 colonies were similar to those in the 1980s: only the number with eggs was reduced. No Razorbill chicks were observed at either Plots A or B on 4 August, and no chicks were seen at Plot C which was observed on most days up until 13 August. By comparison, on GC1 on 3 August we found 93 chicks and 28 eggs, a difference that is highly significant ($\chi^2 = 43.50$, 1 df, $P < 0.001$), indicating that the timing of egg-laying on GC4 was later than on GC1.

The number of Thick-billed Murres on GC4 in 1983 was 866 individuals, but in 1992 we recorded a total of 1585 birds. Elsewhere on the Gannet Clusters, Thick-billed Murre numbers had also increased (D. N. Nettleship and T. R. Birkhead, unpubl. data). The first Thick-billed Murre chick was observed on 1 August 1992. Our qualitative observations suggested that the timing of breeding of Thick-billed Murres on GC4 was similar to that on GC1.

In the 1980s, our most detailed observations were made on Common Murres breeding in two study plots on GC4: CM-A (250 pairs) and CM-B (70 pairs). In 1992, we made observations at CM-A only. However, detailed comparisons between the two time periods were hampered because shifting rocks had altered the configuration of breeding birds and prevented us from re-identifying certain sites. When observations began on 1 August 1992, most Common Murres on CM-A were incubating. Few new eggs were detected subsequently, and no Common Murre chicks had hatched by the time observations ceased on 13 August. Given that the mean incubation period for Common Murres is 33 days and that the mean interval between the first and median hatching dates during the 1980s was about six days (range: 3–8 d) (Birkhead and Nettleship 1987a), this suggests that the median hatching date in 1992 fell between 19 August (at the earliest) and 30 August (latest). The timing of breeding of Common Murres on GC4 was therefore 2–3 weeks later than those on GC1.

The status of breeding sites on CM-A was assessed without disturbing the birds (using Type I observation procedures: see Birkhead and Nettleship 1980). Although it was impossible to determine the precise status of every site, our observations showed that a maximum of 180 sites were occupied by incubating birds in 1992. In the 1980s, the mean hatching success of the 250 pairs on this plot was 85% (Birkhead and Nettleship 1987b), so if the number of breeding pairs had remained the same and hatching success in 1992 was similar to the 1980s, the minimum number of pairs incubating eggs would have been 212 (250×0.85) rather than 180. It is not possible, however, to determine with 100% certainty whether reduction was due to the change in configuration of the study plot or to some other cause such as foxes. However, although certain rocks had moved since 1983, the arrangement of birds in 1992 was not very different (based on careful examination of 1982–1983 study plot photos). That suggests that most of the reduction in the total number of active sites was probably caused by something other than alteration of rock positions.

No observations of Atlantic Puffins on GC4 were made in 1992. All

Black-legged Kittiwakes at the Gannet Islands bred on sea-cliffs on GC4 and GC1—there was no evidence that they had been affected by foxes.

Island GC3.—On GC3 we had no direct evidence for the presence of foxes earlier in the 1992 season, although there were strong circumstantial evidence for the localized effect of some sort of predator. In 1983, we established one Razorbill plot on GC3 with 56 sites: on 2 August 1992 we found 22 eggs (39.3%) and 34 empty sites at this plot. Just as with GC4, laying appeared to have occurred late compared with GC1 (see above). In an adjacent area, however, we found newly hatched Razorbill (and Common Murre) chicks, which we estimated to be 1 or 2 days old, indicating that timing of breeding by some birds was similar to those on GC1.

No Common Murre study plots were established on GC3 during the 1980s. In 1992, therefore, we examined one small group of Common Murres adjacent to the Razorbill study plot. This area contained 113 eggs and 24 (17.5%) chicks, all of which appeared to be one or two days old. We therefore assumed that the first chicks hatched on 31 July 1992. We measured the dimensions of 100 Common Murre eggs that were being incubated: the mean volume index (length $\times$ breadth^2) was 212.68 cm^3 $\pm$ 17.07 SD was smaller than comparable samples measured in the 1980s (the difference between 1992 and 1981 and 1982 was significant [$P < 0.001$], but that between 1992 and 1983 was not [$t = 1.23$, 348 df, $P > 0.05$]). The smaller egg size in 1992 is consistent with that year being a relatively later breeding season (see Table 1).

We also examined a Common Murre breeding area on the northwest side of the island which had been photographed in 1978 (see Birkhead and Nettleship 1980: Fig 6) and in 1983 was estimated to contain about 1000 pairs (Nettleship et al. 1984). In 1992, this area was found to contain 1800 abandoned eggs. Many of the eggs were broken from having rolled off their sites, some had been opened by predators (possibly Great Black-backed Gulls, which breed on all the Gannet Islands), and many were still intact. All eggs were cold, and none appeared to have been incubated. However, among the abandoned eggs was a single group of 10–15 adult Common Murres (on small gravel area between the boulders: lower mid photo, Fig. 6 in Birkhead and Nettleship 1980) with five recently hatched murre chicks which were each attended by one or two adults.

In order to estimate when the murre eggs might have been abandoned, we opened a sample (N = 6) of eggs and measured the total, unstraightened embryo length. The mean volume index of abandoned eggs (212.00 cm^3 $\pm$ 18.43 SD, N = 85) was very similar ($t = 0.26$, 183 df, NS) to that of the 'live' eggs measured on GC3 (see above). Embryos averaged about 2.5 cm in length, which we estimated to be approximately half way (i.e., about 16 days) through the 33 day incubation period (see Mahoney 1979 and Mahoney and Threlfall 1981 for details of aging murre embryos). Assuming the median laying date to be 3 July (see above), the subcolony must have been abandoned somewhere around 19 July 1992. No Atlantic Puffin burrows were examined on GC3 nor were any Thick-billed Murre breeding sites.

DISCUSSION

The effect of resident arctic foxes on breeding seabirds on GC2 and GC5 was dramatic, mainly because of the accessible nature of the breeding sites on these islands. With the exception of most Thick-billed Murres which breed on narrow ledges on steep cliffs at the Gannet Islands (Birkhead and Nettleship 1987b), and were thus inaccessible to foxes, all other species had either abandoned breeding (Common Murres, Razorbills, and possibly Black Guillemots), or like Atlantic Puffins, had attempted to breed but had suffered a high rate of egg loss through a combination of predation by foxes or disturbance. Although we found that between 18 and 25% of active puffin burrows contained either an egg or chick, it seems likely that with continued predation by foxes on GC2 and GC5, few if any Atlantic Puffin chicks would fledge from GC2 or GC5 in 1992.

The situation on GC4, where only 20% of Razorbills appeared to be breeding, and Common Murres were breeding two or three weeks later than on GC1, is more difficult to interpret. The most likely situation is that one or more foxes were present there until the time that Common Murres and Atlantic Puffin first started to lay eggs, probably early July. The presence of a fox on the island may either have deterred some birds from breeding or birds may have laid but then abandoned their eggs. However, since there were no obvious signs of abandoned eggs (as on GC3), the former seems more likely. Once the fox had disappeared from GC4, either by swimming or via a piece of ice, or perhaps after its accidental death, some birds may have resumed breeding. The consequences of late breeding for both Common Murres and Razorbills are not known, but most available evidence suggests that breeding success and the survival of late fledging chicks would be reduced (Nettleship 1972, Birkhead and Harris 1985, Harris 1992).

On GC3, localized abandonment of the Common Murre subcolony, the reduction in the proportion of birds breeding, and the delay in breeding in an adjacent Razorbill subcolony suggests that a fox may have visited this part of GC3 briefly. The location of the abandoned Common Murre subcolony and the adjacent Razorbill study plot are at the point closest to GC2 (see Fig. 1), so it is feasible that a fox crossed from there to GC3. The crossing may have been achieved by walking over concentrated pans of ice or by swimming. Arctic foxes are apparently good swimmers (Nowak 1991), but on all but the calmest days the seasurface current between GC2 and GC3 would have probably deterred a fox from doing this. In fact, it seems unlikely that foxes swam between the islands, as we saw no sign of them doing so during our visit. A more likely scenario is that the presence of sea ice and its movements between the islands allowed foxes to make a brief visit to GC3 around mid-July and to leave from GC4 sometime earlier.

The Gannet Islands are all relatively low lying, with relatively few steep cliffs, and the maximum height of these is 66 m. As a result, all the alcid species, except for most of the Thick-billed Murres and a few Common Murres and Razorbills, breed in very accessible locations. This suggests that the occurrence of arctic foxes or other important terrestrial predators at this colony must be an extremely infrequent event. In other seabird colonies, areas where terrestrial predators occur regularly, such as mainland sites, most seabirds are forced to breed in inaccessible sites, usually in rock fissures or crevices or on steep vertical cliffs (Fisher and Lockley 1954, Freuchen and Salomonsen 1958, Larson 1960, Tuck 1961, Lack 1968, Salomonsen 1979, Petersen 1982, Bailey 1993).

The occurrence of arctic foxes at the Gannet Islands may have been a chance event associated with heavy winter ice and a low in the abundance of small rodents on the mainland: i.e., Ungava lemming cycle (Lewis 1923, Elton 1942, Harper 1960, Vibe 1967, Banfield 1974). Such a shortage in food availability is known to cause the foxes to undergo extensive movements and shift toward the coast and out onto the sea ice (Banfield 1974, Nowak 1991). In fact there was an arctic fox invasion along the north shore of the Gulf of St. Lawrence during the 1987–1988 winter (Canadian Wildlife Service-Quebec Region files) that subsequently adversely affected several seabird island sanctuaries within the region before they were removed (G. Chapdelaine, Can. Wildl. Serv., pers. comm.). Nearshore locations in coastal Labrador have more frequent visitations by foxes and other four-legged predators than those farther offshore such as the Gannet Clusters. However, the fact that in 1992 there were four adult foxes and one pair was breeding, suggests a resident and expanding population that may also be related to winter 1987–1988.

If the foxes are successful and remain on the Gannet Islands, most seabird species eventually will be eliminated, as has occurred on some of the Aleutian Islands and elsewhere in Alaska (Bailey 1993). This raises an interesting point regarding the life history strategies of long-lived seabirds. Our observations suggest that foxes may have been on GC2 and GC5 for one or more seasons prior to 1992, perhaps since the winter of 1987–1988. As far as we could tell, the adult Razorbills were still firmly associated with their breeding subcolony, visiting sporadically, but spending a lot of time on the sea immediately adjacent to the subcolony. It is interesting to speculate how long a bird could afford to wait before deserting its subcolony and attempting to find a breeding site elsewhere. Presumably part of the answer to this question depends upon the availability of other nearby colonies or other locations where new colonies could start and the length of time the disturbance factor is likely to persist at the present site. It may be significant that most Razorbills were continuing to associate with the Gannet Islands, despite their inability to breed owing to the presence of foxes, simply because suitable alternative sites are extremely scarce or the foxes are unlikely to remain and disperse to islands within the Gannet Island archipelago. There are several reasons for thinking that one or both of these might be the case. The Gannet Islands are farther offshore than any other islands along this stretch of coast, a factor which may increase the foraging efficiency of the birds, but also provide them with a relatively high degree of safety from terrestrial predators, including people (for details, see Nettleship and Evans 1985). Short-term losses may be offset by gains over the longer term, especially if the foxes do poorly and cease to reproduce successfully, one consequence of which might be to abandon the islands during winter when conditions allow (Banfield 1974, Nowak 1991). The fact that the Gannet Islands seabird community has been known for more than a century and that foxes do not seem to be a regular part of the Gannet Islands' terrestrial ecosystem (based on existing information: no previous records of foxes—either direct observations or the presence of scats,—over a period of at least 70 years) suggest that conditions necessary for establishment of a permanent fox population on the Gannet Islands are deficient and that the present animals will soon disappear since there is no alternative prey other than a very small population of passerines during summer and a small population of deer mice (*Peromyscus maniculatus*) on GC4. The small litter size (2 instead of the usual 6–12, Nowak 1991) of the pair on GC2 and nonbreeding by those on GC5 support this prediction, though the pair on GC5 could both have been the same sex or infertile. After consultation with the Canadian Wildlife Service and the Newfoundland-Labrador Seabird Ecological Reserve Committee, it was decided that because of the status of the Gannet Islands, the foxes should be removed. Accordingly, in late September 1992, an adult female and two pups on GC2 and one adult of GC5 were shot under permit. A visit to GC2 and GC5 in May 1993 revealed that no foxes were present, nor were there any tracks in the snow or scats, which indicates that the remaining foxes had not remained or had failed to survive.

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